WOOD ANATOMY OF AMPHIACHYRIS, AMPHIPAPPUS, THUROVIA, GYMNOSPERMA, AND THE XANTHOCEPHALUM COMPLEX

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The problem of delimiting *Amphipappus*, *Amphiachyris*, *Greenella*, *Gutierrezia*, *Gymnosperma*, *Xanthocephalum*, and *Thurovia* (Compositae) has been reviewed by Gray (1873), Bentham and Hooker (1873), Rose (1895), Nelson (1934), Porter (1943), Shinners (1950), Solbrig (1960), Correll and Johnston (1970), and Ruffin (1971). Unfortunately, the phylogenetic relationship of the genera is still an open question. This is the second paper in a multiphase investigation intended to assemble new evidence toward a more satisfactory taxonomic treatment of the genera. Comparative morphological and anatomical studies—of ray and disc florets, phyllaries, receptacle, achene, pappus, style, and leaves—and recent cytological findings reported in the previous article (Ruffin, 1971) disclosed evidence favoring the merger of the previous distinct *Xanthocephalum*, *Gutierrezia*, and *Greenella* into one coherent genus and maintaining *Gymnosperma*, *Amphiachyris*, *Amphipappus*, and *Thurovia* as distinct genera. *Xanthocephalum*, the earliest name in the group merged, is used throughout this report to include the previously distinct genera.

Although the details of wood anatomy presented here are by no means conclusive it is hoped that they will be of value in properly interpreting the limits of and evolutionary relationship among the genera.

MATERIALS AND METHODS

Most wood samples were sectioned between 15-20 microns on a sliding microtome and were stained with safranin or with safranin and fast green with tannic acid followed by ferric chloride. When material allowed, macerations were made using Jeffrey's 10% chromic acid-10% nitric acid solution for those wood features difficult to measure from sectioned material. For wood samples taken from herbarium sheets, 71 measurements were made from each collection except *Xanthocephalum ramulosa* and *X. linearifolium* where only 51 were made due to inadequate longitudinal sections. *Thurovia triflora* lacked wood rays; thus other wood features totalled 51 measurements. Wood averages from field material represent 20 measurements for each character, with the exception of widest vessel diameter, taken from two individuals in each population. In all, 4,697 measurements were made.

In order to measure characters such as average diameter of vessels,

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average number of vessels per group, average length of vessel elements, etc., where there are many measurable elements per section, a random sample of such elements was measured. A starting point for scanning a slide was chosen by using random coordinates on the mechanical stage. Moving the slide horizontally (from right to left), I scanned the microscope field between two major lines on an ocular micrometer. Each element measured was given an arbitrary reference point. Whenever these arbitrary points fell within the two lines on the ocular scale, those characters were measured or counted.

OBSERVATIONS AND RESULTS

Table 1 summarizes qualitative and quantitative features for the species studied. Tables 2 thru 9 present a summation of quantitative characters in each of the genera. *Xanthocephalum ramulosum* and *X. linearifolium* have been omitted from Table 1 because of reasons stated elsewhere. However, those features that could be measured are included in the averages of the various genera. In addition, features not included in the tables will also be discussed.

Vessels. Although I did not attempt to determine the exact frequency of vessels seen in a transection, vessels appear to be very numerous in most species of *Xanthocephalum* (*X. gymnospermoides*, *X. sarothrae*, *X. microcephalum*, *X. texanum*, *X. wrightii*). The vessels are also distributed in radial rows in the majority of *Xanthocephalum* species studied. *Xanthocephalum sericocarpum* shows some tangential pairs, a few solitary vessels, and a few short radial rows. In *X. microcephalum* and *X. sarothrae*, solitary vessels as well as long radial chains are present. A significant condition in the latter two species is a tendency toward ring porosity. In each species the ring-porous condition takes the form of more numerous and larger vessels in the late wood (Fig. 1). Also noteworthy is the presence of vascular tracheids in the latter two species.

Extensive grouping of vessels also characterizes most *Xanthocephalum* species. In a number of instances as many as 12 vessels per group were seen. In those members of the genus showing the ring-porous condition, the early wood exhibit smaller numbers of vessels per group whereas the late wood show extreme grouping. Vessel grouping is, however, less extensive in *X. centauroides*, *X. mandonii* spp. *mandonii*, and *X. sericocarpum*. Vessels in the latter species are in groups of two to eight, mostly two to five.

In *Amphiachyris*, vessels appear numerous in all species. Distribution and amount of vessel grouping are diverse and not so extensive as in most species of *Xanthocephalum*. This genus is characterized by solitary vessels, short radial rows of two to six vessels, and some tangential pairs. *Amphiachyris amoenum* var. *amoenum* and *A. amoenum* var. *intermedium*, in every population studied, tend toward a ring-porous condition. Both have been described as annuals, but a simple type of growth ring is represented in which growth appears to be accompanied by diminution in diameter of

Table 1. Comparative features of the wood in Amphiachyris, Amphipappus, Gymnosperma, Thurovia, and Xanthocephalum

Species	Age	Collection	diameter of widest vessel µm	average diameter of vessels µm	average length of vessel elements µm	average diameter of libriform fibers µm	average length of libriform fibers µm	fiber dimorphism	ray crystals	average height of multiseriate rays, mm	ray cells isodiametric to procumbent	ray cells isodiametric to erect	average number cells of maximum ray width
Amphiachyris amoenum													
var. *amoenum*	2?	Ruffin 7033	62.5	34.6	165.7	11.5	397.1	+	—	1.3	+	+	3.7
	3?	Ruffin 7034	57.5	37.0	167.6	11.6	425.5	+	—	1.5	+	+	4.0
	2?	Ruffin 7035	66.0	33.0	185.5	11.9	453.3	+	—	1.4	+	+	3.5
A. amoenum var.													
intermedium	2?	Ruffin 7030	62.5	38.0	176.2	11.1	424.4	+	—	1.6	+	+	4.0
	2?	Ruffin 7031	67.5	35.7	185.3	10.8	413.4	+	—	1.3	+	+	3.8
	2?	Ruffin 7032	72.5	42.0	156.1	11.6	431.5	+	—	1.1	+	+	4.3
A. dracunculoides	1	Ruffin 7036	55	37.3	119.0	13.2	455.2	+	—	.985	+	+	3.2
	1	Ruffin 7037	57.5	39.5	136.0	11.5	450.7	+	—	.852	+	+	2.8
	1	Ruffin 7038	60	38.1	139.8	15.4	473.7	+	—	.943	+	+	2.6
	1	Ruffin 7039	57.5	33.9	135.0	13.7	511.7	+	—	.686	+	+	2.6
Amphipappus fremontii	7	Clokey 5962	50	29.0	119.5	10.6	304.5	—	—	1.2	+	+	4.0
Gymnosperma													
glutinosum	8	Ruffin 7010	62.5	31.3	133.9	10.2	133.8	—	—	1.0	+	+	3.2
	7	Ruffin 7011	67.5	29.5	111.8	10.2	359.9	—	—	.888	+	+	3.6
	9	Ruffin 7012	67.0	34.0	110.9	11.2	375.6	—	—	.946	+	+	3.4

Table 1. (Cont.)

	8	Ruffin 7013	62.5	29.2	122.0	11.1	372.0	—	—	1.0	+	+	3.6
Thurovia triflora	1	Tharp 280	50	31.0	116.0	10.8	292.0	—	—	—	—	—	—
Xanthocephalum centauroides	1	Palmer 501	45	34.5	128.0	11.8	344.5	—	+	1.7	+	+	3.7
X. gymnospermoides	1	Ruffin 7024	72.5	46.5	187.5	14.1	471.5	—	—	1.3	+	+	3.6
	1	Ruffin 7025	77.5	43.1	213.2	13.2	455.1	—	—	.943	+	+	3.1
	1	Ruffin 7026	82.5	38.5	197.5	13.3	463.2	—	—	1.0	+	+	3.5
X. mandonii spp. *mandonii*	3	Venturi 8156	48.0	29.5	95.5	10.1	303.5	—	—	.75	+	+	3.3
X. microcephalum	7	Ruffin 7005	48.5	20.7	122.8	13.0	290.8	—	+	.933	+	+	2.9
	9	Ruffin 7006	50	23.4	132.1	11.4	275.2	—	+	.895	+	+	2.8
X. sarothrae	4	Ruffin 7001	49.5	26.8	69.3	10.1	278.7	—	+	1.3	+	+	5.8
	3	Ruffin 7002	47.0	30.0	75.2	9.5	284.7	—	+	1.1	+	+	5.6
	2	Ruffin 7003	43.5	24.9	72.8	10.2	299.7	—	+	1.3	+	+	5.0
	3	Ruffin 7004	49.0	26.6	70.7	10.2	292.2	—	+	1.3	+	+	5.7
X. sericocarpum	1	Palmer 143	50	31.0	110.5	10.2	263.5	—	—	2.1	+	+	4.5
X. texanum	1	Ruffin 7007	70	33.2	141.5	11.1	397.8	—	—	.538	+	+	2.4
	1	Ruffin 7008	65	32.8	127.6	10.3	419.6	—	—	.531	+	+	2.9
	1	Ruffin 7009	67	28.4	157.8	12.0	439.2	—	—	.531	+	+	3.1
X. wrightii	1	Ruffin 7020	50	23.7	127.0	11.9	442.7	—	—	.421	+	+	2.2
	1	Ruffin 7021	49.0	24.5	139.5	12.9	436.9	—	—	.446	+	+	2.0
	1	Ruffin 7022	50.5	26.0	131.5	13.0	460.5	—	—	.462	+	+	1.9
	1	Ruffin 7023	50	23.7	141.0	13.9	445.2	—	—	.480	+	+	1.6

Table 2. Comparison of vessel element diameter in Xanthocephalum, Amphiachyris, Gymnosperma, Amphipappus, and Thurovia

Genus	Number of taxa	Number of individuals	Range μm	Range of means μm	Mean μm
Xanthocephalum	10	37	10-75	18.5-42.7	31.7
Amphiachyris	3	20	10-70	34.8-38.5	36.8
Gymnosperma	1	4	8-60	—	31.0
Amphipappus	1	1	10-50	—	29.0
Thurovia	1	1	20-50	—	31.0

Table 3. Comparison of vessel element length in Xanthocephalum, Amphiachyris, Gymnosperma, Amphipappus, and Thurovia

Genus	Number of taxa	Number of individuals	Range μm	Range of means μm	Mean μm
Xanthocephalum	10	37	40-330	72.0-199.4	118.5
Amphiachyris	3	20	45-300	132.4-172.5	159.2
Gymnosperma	1	4	50-210	—	119.6
Amphipappus	1	1	90-150	—	119.5
Thurovia	1	1	90-165	—	116.0

vessels (Fig. 3). This condition was not present in any of the populations of *A. dracunculoides*. Vascular tracheids were not observed in any species of *Amphiachyris*.

Vessels in *Gymnosperma glutinosum* are very numerous. Vascular tracheids also occur in the xylem. Degree of ring porosity in the wood is strongly portrayed. In terms of vessel distribution, no one pattern seem to predominate. Numerous solitary vessels, tangential clusters, and short radial rows are all pronounced. Grouping of vessels is not so extensive as in *Xanthocephalum* but does resemble the grouping in *Amphiachyris*.

In *Amphipappus*, vessels are also numerous. Some vessels appear solitary but most show extensive grouping in radial and tangential chains (Fig. 4). The ring-porous condition is also well developed. Large vessels are seen in early wood while narrower vessels and vascular tracheids occur in late wood.

Vessels in wood of *Thurovia* show a somewhat unusual pattern. Most large vessels occur in primary tissues of the xylem while the more numerous narrower vessels and vascular tracheids are in the later-formed xylem tissue. Because of the difficulty of distinguishing vascular tracheids from narrow vessel elements, patterns of vessel distribution and vessel grouping in *Thurovia* were very difficult to estimate.

Mean vessel length and diameter for each species, range, range of means, and the mean for all species studied in each of the genera are represented in Tables 1, 2, 3. Mean vessel diameter and mean vessel element length in

Table 4. Comparison of libriform fibers diameter in Xanthocephalum, Amphiachyris, Gymnosperma, Amphipappus, and Thurovia

Genus	Number of taxa	Number of individuals	Range µm	Range of means µm	Mean µm
Xanthocephalum	10	37	10.0-15.8	9.0-13.5	10.9
Amphiachyris	3	20	9.1-18.2	11.1-13.4	12.0
Gymnosperma	1	4	6.8-13.6	—	10.6
Amphipappus	1	1	9.1-11.3	—	10.6
Thurovia	1	1	9.1-11.3	—	10.9

Table 5. Comparison of libriform fiber length in Xanthocephalum, Amphiachyris, Gymnosperma, Amphipappus, and Thurovia

Genus	Number of taxa	Number of individuals	Range µm	Range of means µm	Mean µm
Xanthocephalum	10	37	210-556	263.5-463.2	340.1
Amphiachyris	3	20	240-695	423.1-472.8	440.4
Gymnosperma	1	4	270-480	—	310.3
Amphipappus	1	1	250-340	—	304.5
Thurovia	1	1	250-340	—	292.0

the various genera are quite similar except in *Amphiachyris*. In *Amphiachyris* mean vessel diameter and mean vessel element length exceed the figures noted in the other genera. Vessel-element perforations, in all the genera, were simple. In any given sample the end walls of the vessels may vary from transverse to oblique. Intervascular pits are 3–5 μm in diameter for all of the species considered and are alternately arranged.

Helical thickenings are found on the inner vessel wall of many of the species studied. Helical thickening, however, is not noticeably present on the vessel wall of any of the species of *Amphiachyris*. These thickenings are especially conspicuous on walls of the narrower vessel elements and on walls of vascular tracheids in *Xanthocephalum sarothrae*, *X. microcephalum*, *Gymnosperma*, *Thurovia*, and *Amphipappus*. In all of the above species except *Amphipappus* these helical thickening are grooves connecting the apertures of pits. In *Amphipappus*, coarse bands were noted on each side of a series of pits forming a helix on the inner vessel wall. None of the elements of the xylem of *Amphiachyris* and *Gymnosperma* was storied. Except for the vascular tracheids present in *Xanthocephalum sarothrae*, *X. microcephalum*, *Thurovia*, and *Amphipappus*, none of the elements in the xylem of these genera appeared storied.

Libriform fibers. Average dimensions of libriform fibers appear related to dimensions of vessel elements. This is indicated by the fact that shorter fibers occur in those species with shorter, narrower vessel elements. This correlating of average dimensions is clearly shown by Tables 2, 3, 4, 5. The

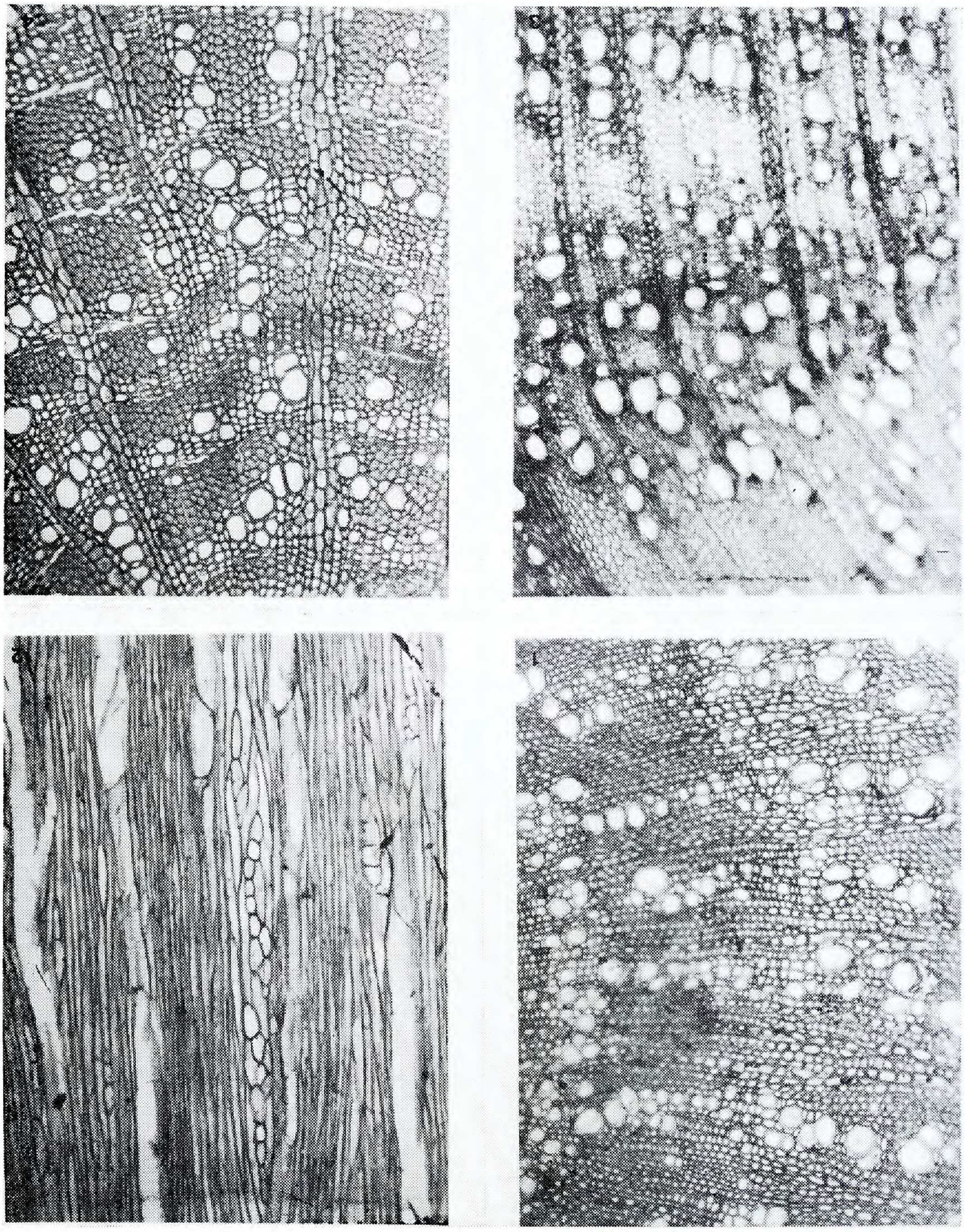

Fig. 1. Cross-section of *Gutierrezia microcephala* wood showing ring-porous condition. Note solitary as well as long radial chains of vessels, X89. 2. Tangential section of *Xanthocephalum wrightii* wood showing short and widely spaced rays, X89. 3. Cross-section of *Amphiachyris amoenum* wood where growth appears to be accompanied by diminution of vessels, X89. 4. Cross-section of *Amphipappus fremontii* wood showing wide rays, arrangement, and distribution of vessels, X89.

Table 6. Comparison of maximum ray width in Xanthocephalum, Amphiachyris, Gymnosperma, Amphipappus, and Thurovia

Genus	Number of taxa	Number of individuals	Range	Range of Means	Mean
Xanthocephalum	8	35	1-14 cells	1.9-5.5 cells	3.5 cells
Amphiachyris	3	20	1-6 cells	2.8-4.0 cells	3.5 cells
Gymnosperma	1	4	1-6 cells	—	3.5 cells
Amphipappus	1	1	2-6 cells	—	4.0 cells
Thurovia	1	1	No rays	—	—

Table 7. Comparison of multiseriate ray height in Xanthocephalum, Amphiachyris, Gymnosperma, Amphipappus, and Thurovia

Genus	Number of taxa	Number of individuals	Range mm	Range of means mm	Mean mm
Xanthocephalum	8	35	0.23-3.0	1.1 -2.1	1.1
Amphiachyris	3	20	0.25-2.7	0.86-1.4	1.2
Gymnosperma	1	4	0.23-2.1	—	.96
Amphipappus	1	1	0.37-2.8	—	1.2
Thurovia	1	1	No rays	—	—

longer vessel element in *Amphiachyris* parallels the dimensions given for fiber length in this genus. Also, the large vessel elements in *Xanthocephalum gymnospermoides* correlates with the long fibers present in this species.

Amphiachyris is also distinct from the other genera in that fiber dimorphism occurs in the wood of all three taxa. Extremely long, thick-walled fibers and shorter fibers occur within the same wood samples. As pointed out by Anderson (1963) "this condition may be indicative of a trend toward greater parenchymatization which in turn may be related to a more herbaceous habit." Even though slight differences exist in fiber diameter both among as well as within genera, these fibers are considered to be somewhat narrow for the Astereae. According to Carlquist (1960) the diameter of libriform fibers of most Astereae is 20–35 μm. Fiber walls of all species studied are 2.3–5.1 μm thick.

Rays. According to Carlquist (1962a) elimination or loss of uniseriate rays is common in Compositae. *Xanthocephalum* demonstrates this clearly. In only three species, *X. wrightii*, *X. gymnospermoides*, and *X. texanum*, were uniseriate rays abundant. In no instances, however, were uniseriate rays as frequent as multiseriate ones. Uniseriate rays in the three species are four to six cells high. In all of the other species of *Xanthocephalum* studied, uniseriate rays were completely absent or rare and very limited in height (usually one cell high).

Average ray width in *Xanthocephalum* is wide (two to four cells) to very wide (four to six cells). *Xanthocephalum wrightii*, where most rays are bi-

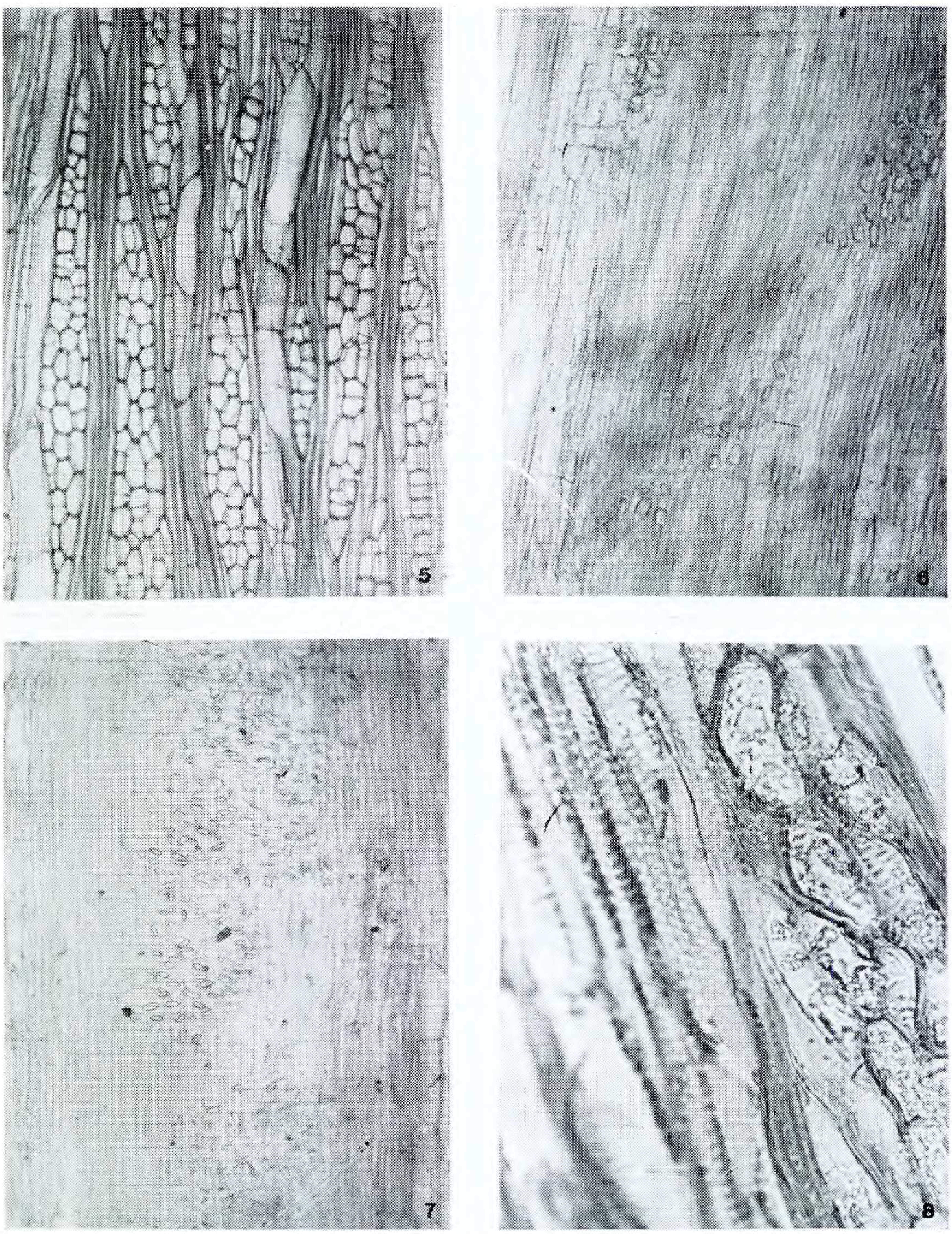

Fig. 5. Tangential section of *Xanthocephalum gymnospermoides* showing high and wide rays, X89. 6 - 8. Longitudinal sections showing prismatic crystals in ray cells: 6. *Gutierrezia microcephalum*, 7. *Gutierrezia sarothrae*, 8. *Xanthocephalum centauroides*, X89.

Table 8. Comparison of vessel element length in annuals*—Xanthocephalum, Amphiachyris, and Thurovia

Genus	Number of taxa	Number of individuals	Range µm	Range of means µm	Mean µm
Xanthocephalum	4	21	50-330	110.5-199.4	146.7
Amphiachyris	3	20	45-300	132.4-172.5	159.2
Thurovia	1	1	90-165	—	116.0

* *Amphiachyris amoenum* var. *amoenum* and *A. amoenum* var. *intermedium* may be biennials.

Table 9. Comparison of vessel element length in perennials—Xanthocephalum, Amphipappus fremontii, and Gymnosperma

Genus	Number of taxa	Number of individuals	Range µm	Range of means µm	Mean mm
Xanthocephalum	6	16	40-175	72.0-128.0	99.7
Amphipappus fremontii	1	1	90-150	—	119.5
Gymnosperma	1	4	50-210	—	119.6

seriate, and *X. texanum* are characterized by the former condition while the remainder of the species in this genus are characterized by the latter pattern. Ray width in species of *Xanthocephalum* seems to correlate with ray height: species characterized by wide rays also have high rays. In contrast, those species with narrower rays are limited in their vertical extent. *Xanthocephalum gymnospermoides* (Fig. 5) and *X. sarothrae* show the highest rays in this genus while *X. wrightii* (Fig. 2) shows the least amount of ray height development. In terms of ray number and distribution, as seen in tangential view, all species studied except *X. wrightii* showed numerous closely-spaced rays. In *X. wrightii* the rays are less numerous and widely dispersed.

Uniseriate rays were lacking in *Amphiachyris amoenum* var. *amoenum* and *A. amoenum* var. *intermedium* and for the most part scarce in *A. dracunculoides*. When present, they are one to four cells high. Ray cells are one to four cells wide in *A. dracunculoides* and two to six cells wide in the other two taxa. Ray height is moderately high in all three taxa. Ray height is 0.4–2.7 mm in *A. amoenum* var. *amoenum* and *A. amoenum* var. *intermedium* and 0.25–1.8 mm in *A. dracunculoides*.

In wood of *Gymnosperma glutinosum* uniseriate rays one to two cells high were occasionally observed. The rays were one to six cells wide. Average ray height for the populations studied is 0.88–1.0 mm.

In *Amphipappus fremontii* no uniseriate rays were observed in the wood. The multiseriate rays ranged from two to six cells wide and 0.37–2.8 mm high.

Rays of the genera studied are heterocellular, having both erect and procumbent cells. However, both multiseriate and uniseriate rays are absent in wood of *Thurovia*. Carlquist (1966) lists the few genera of Compositae in which rayless woods have been found; *Thurovia* can now be added to the list. Barghoorn (1941) states clearly conditions which may promote raylessness.

Resin deposits and crystals. Resin deposits are noticeably present in wood of all species studied except *Xanthocephalum gymnospermoides*, *X. ramulosum*, *Thurovia triflora*, and *Amphiachyris dracunculoides*. Carlquist (1960) had previously described the conspicuousness of these resinous deposits in *X. microcephalum* (as *Gutierrezia microcephala*). In many instances numerous vessels are entirely filled with resinous contents.

Carlquist (1960) also described the presence of prismatic crystals in the ray cells of *X. microcephalum* (Fig. 6). In my investigation, crystals were also observed in *X. sarothrae* (Fig. 7) and *X. centauroides* (Fig. 8). These crystals are much like those figured by Carlquist for *X. microcephalum*. Conspicuous crystals were not observed by me in any of the other species.

DISCUSSION AND CONCLUSIONS

With the wood data, it seems easier to show levels of specialization than to indicate relationships. However, there are some clear distinctions worthy of mention.

The genus *Amphiachyris* is distinctive because of its large vessels, the longer and wider libriform fibers, and the presence of fiber-dimorphism. Even when average vessel-element length of annuals is compared, *Amphiachyris* maintains this distinctiveness. In contrast, *Thurovia*, in addition to its peculiar distribution of vessels, shows the shortest average vessel element length among the annuals (Tables 3, 8). The large vessel-element length among annual species of *Xanthocephalum* is due solely to the large xylem elements present in *X. gymnospermoides*. The fact that relatively long and wide vessel elements occur in *X. gymnospermoides* is very interesting. Perhaps these large elements of the xylem, the larger leaves, little branched inflorescence, and the large chromosome number ($n=6$) qualify this species as the most primitive member in the genus. However, when annuals and perennials are combined, even though some vessel elements and libriform fibers in *Xanthocephalum* are wider and longer than those in *Gymnosperma*, *Amphipappus*, and *Thurovia*, there are little differences in the mean for these characters.

Helical sculpturing in vessels and vascular tracheid of the secondary xylem offers another distinctive feature. No prominent helical sculpturing occurs in *Amphiachyris*. The coarse band wall relief in *Amphipappus* is sufficiently distinct from the continuous groove pattern noted in *Gymnosperma*, *Thurovia*, and certain species of *Xanthocephalum*.

Somewhat high rays characterize all of the genera. Wide heterocellular rays are also characteristic. The fact that *Thurovia* lacks wood rays certainly sets it apart from the other genera studied.

This treatment of the genera is by no means conclusive. Additional biosystematic studies of the taxa are needed to more accurately reflect their evolutionary history. However, the distinctiveness described above when coupled with the cytological, anatomical, and morphological evidence reported earlier (Ruffin, 1971) provides one more line of evidence supporting the distinctiveness of *Gymnosperma*, *Amphiachyris*, *Amphipappus*, and *Thurovia* and unifying reasons for merging *Xanthocephalum*, *Gutierrezia*, and *Greenella*.

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